
PATTERNS OF VASCULAR PLANT DIVERSIFICATION IN THE FOSSIL RECORD: PROOF AND CONJECTURE

Karl J. Niklas¹

ABSTRACT

An analysis of historical trends in diversification can suffer from a variety of defects and limitations. Among these is the potential failure of genus and family compilations to yield sufficient information on biological events, such as mass species extinctions. Another is the inadequacy of taxonomically based estimates of diversification to reveal patterns in changing community structure and morphology, which are important in evaluating adaptive evolution. These deficiencies are examined for the plant fossil record and by means of computer simulations of mass extinction events. Comparisons among species, genus, and family diversification patterns reveal qualitative differences sufficient to warrant caution in the use of taxonomic ranks above the species level. However, genus tabulations appear to be an adequate surrogate database for inferring patterns of species origination. Computer simulations revealing patterns of family extinctions may be inadequate for evaluating mass species extinction events since peaks in species and family extinctions rarely, if ever, coincide. A pluralistic approach to evaluating diversification is advocated involving the examination of biotic changes within assemblages and trends in morphological, anatomical, and reproductive evolution.

The notion of *diversity* in paleontology differs little from its use in ecological studies (Raup & Stanley, 1971; Whittaker, 1977). Diversity can be defined as the number of taxa in a community or as the synthetic characteristic of taxonomic richness and equitability, i.e., the relative evenness of the importance values of taxa within a sample (Lloyd & Ghelardi, 1964). However, the nature of the fossil record precludes a direct comparison of diversity between past and present biotas (Krassilov, 1975; Padian & Clemens, 1985). In ecology, taxonomic richness reflects the number of species in a sample of standard size, while measures of equitability involve some gauge of the abundance or productivity of one species divided by the importance values of all other species within the sample (Pielou, 1977). By contrast, fossil assemblages usually reflect time-averaged samples of a geographically ill-defined area. Further, terrestrial organisms are preserved where they were buried, not generally where they lived, and most often after significant periods

of decomposition (cf. Niklas et al., 1980; Padian & Clemens, 1985). Frequently, transport to sites of burial results in the disarticulation of land plants and animals, and in deposition of parts in sedimentologically different microenvironments (cf. Kidwell, 1986). Consequently, there is great difficulty (1) in recognizing a species from its parts, (2) reassembling the components of a community, and thereby (3) arriving at a measure of diversity that is comparable to contemporary ecological studies (Raup, 1976, 1979; Niklas et al., 1980; Knoll, 1984; Benton, 1985).

Despite its limitations, the fossil record provides a potentially valuable perspective on a number of evolutionary issues. The paleontologist can compare patterns of diversification over billions of years of Earth's history and can track the origin, radiation, and eventual taxonomic diminution of organisms that no longer exist or are rare in present biotas. Although the nature of paleontological data defines the temporal and taxonomic resolution with which evolutionary issues can be ad-

¹ Section of Plant Biology and Section of Ecology and Systematics, Cornell University, Ithaca, New York 14853, U.S.A.

dressed, recognition of large-scale patterns that develop, change, and disappear over long intervals of time confers a perspective that augments neontological studies.

This paper is concerned with changes in tracheophyte diversity over the last 400 million years of the Phanerozoic. The fossil record of terrestrial vascular plants is reviewed and discussed within the context of large-scale patterns in composition and taxonomic richness of assemblages through time. The bulk of the data to be discussed has been presented elsewhere in a variety of forms (Niklas et al., 1980, 1985; Tiffney, 1981; Knoll, 1984, 1986; Knoll et al., 1984). Consequently, many facets of tracheophyte diversification will be referenced but not discussed in detail. The principal focus of this paper will be on the limitations of the data and on the qualitative statements about plant evolution that can be made from an inherently imperfect fossil record.

LARGE-SCALE CHANGES AND TAXONOMIC LEVEL

The species is the taxonomic level of choice for determining changes in diversity through geologic time. However, species-level compilations present a variety of procedural difficulties, the most significant of which involve sampling errors (Signor & Lipps, 1982; see also Pease, 1985). Comparisons of global patterns in species diversification with higher taxonomic levels are desirable, because they provide insights into the information to be gained or lost by each type of compilation.

The upper panel of Figure 1 shows a plot of the total species-richness of vascular plants through the Phanerozoic. The data are taken from primary paleobotanical citations tabulated by Niklas et al. (1985) and are segregated into three major categories of tracheophytes: pteridophytes, gymnosperms, and angiosperms. The plot shows a Silurian to mid-Devonian radiation of primitive pteridophytes followed by a Carboniferous proliferation of more advanced or derived pteridophytes and early gymnosperms. A Permo-Triassic decrease in overall diversity precedes a more

or less constant level of species number until the middle of the Cretaceous when angiosperms begin to radiate. Diversity of pteridophytes decreased during the Permo-Triassic and reached a relatively constant level throughout much of the Mesozoic and Cenozoic. With the advent and proliferation of angiosperms, the number of gymnosperm species decreased significantly through much of the late Cenozoic.

The lower panel in Figure 1 shows large-scale temporal patterns in diversity at the family level. These data (from Knoll, 1984) were compiled independently from the data on species from Niklas et al. (1980). Data for pteridophytes and gymnosperms are not segregated, thus providing for direct comparisons between species- and family-level diversity for nonangiosperms and for angiosperms. Differences in the diversity between Devonian and Carboniferous families are less pronounced than those seen in the top panel. As Knoll (1984) noted, the number of species in late Paleozoic families is higher than in early Paleozoic families, presumably due to the appearance of more complex or numerous morphological and anatomical features upon which species can be based. Ordinal changes in plant diversity compiled by Knoll (1984) conform in large measure to the trends seen in the family diversity plot.

Despite the differences between species and family diversity, it is evident that the number of vascular plant taxa increased throughout much of the Paleozoic and has accelerated during the Cenozoic with the advent of angiospermy.

The value of comparing diversity among different taxonomic levels can be further illustrated by examining data for a specific group rather than the entire domain of tracheophytes. The selected group ought to have a fossil history that spans the Phanerozoic and thus obviates any idiosyncratic feature of a geologic period. Three major groups of vascular plants have a virtually continuous fossil record since the Upper Devonian: lycopods, sphenopsids, and ferns (Stewart, 1983). Of these three groups, the ferns are the most abundant through time. Hence, they

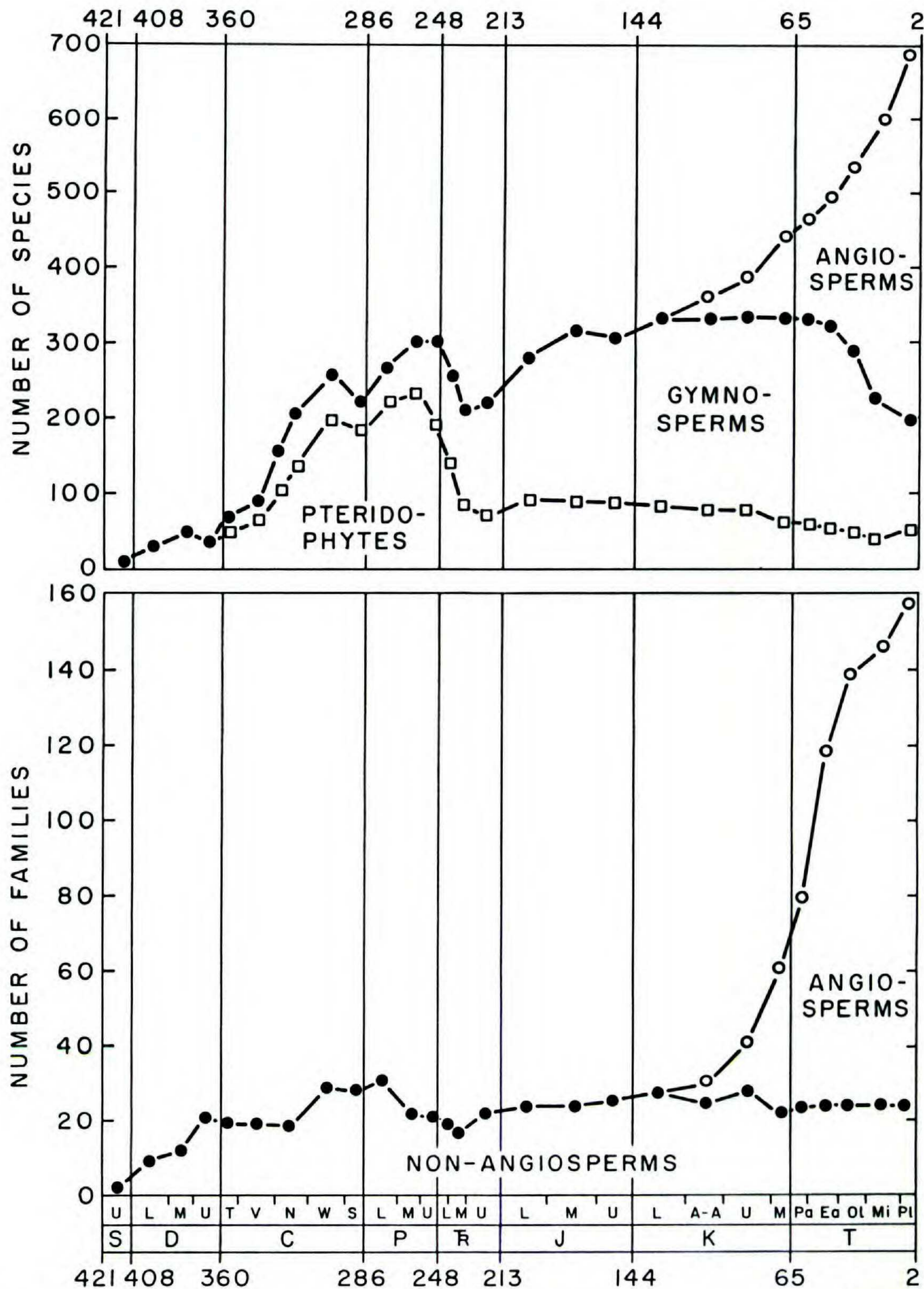


FIGURE 1. Large-scale changes in diversity of tracheophytes at the species- and family-level (upper and lower panels, respectively) recorded per epoch through the Phanerozoic. Species global diversity data were taken from Niklas et al. (1980, 1985); family diversity data are redrawn from Knoll (1984). The time-scale is that of Harland et al. (1982): For the Carboniferous (C), T = Tournaisian, V = Visean, N = Namurian, W = Westphalian, S = Stephanian; for the Cretaceous (K), L = Berriasian-Barremian, A-A = Aptian-Albian, U = Cenomanian-Campanian, and M = Maastrichtian.

are convenient for comparing differences in diversity based on compilations of species, genera, and families. The most complete treatment of fossil ferns is that of Boureau (1970). Unfortunately, this does not reflect recent advances in taxonomy nor does it present a critical evaluation of stratigraphic oc-

currences (see for example Phillips, 1974; Stewart, 1983). Nonetheless, the data contained within this volume are useful because they are easily accessible and reflect the state of paleobotanical knowledge as compiled in a single reference. Accordingly, the data for fossil ferns are dealt with here solely for the

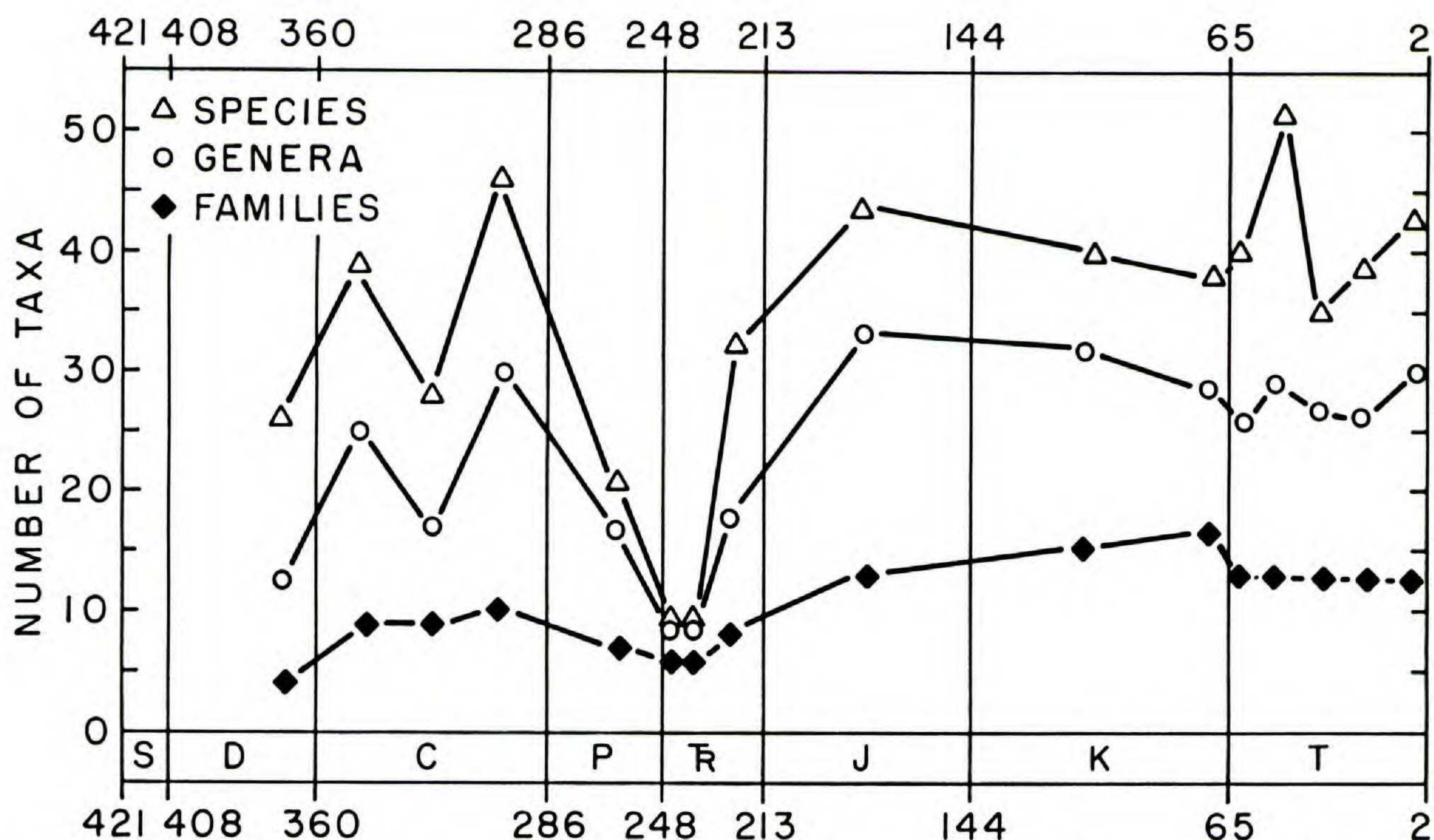


FIGURE 2. Taxonomic diversification of ferns based on data compiled by Boureau (1970). Stratigraphic resolution of species, genus, and family occurrences from the source is coarser than that of species diversity plotted in Figure 1. Consequently, the time-scale of this figure is less precise than desirable.

purpose of comparing the qualitative diversity measurements made at different taxonomic levels within a major plant group.

Figure 2 shows the total diversity of fossil ferns based on species, genus, and family compilations. Since the citations given in the data sets are rarely more specific with regard to stratigraphy than lower or upper, middle, and lower divisions of each period, the resolution of the geologic scale is necessarily more crude than desirable and not directly comparable to those given in Figure 1.

Peaks in the species diversity of ferns occur in the Lower and Upper Carboniferous, the Middle Jurassic, and in the Eocene. The maximum number of fossil fern species is recorded in the Eocene. Species numbers significantly decrease in the Middle Carboniferous, Lower and Middle Triassic, and in the Oligocene. Generic tabulations reveal similar peaks and valleys in diversity as those seen in the species data; however, the overall diversity maximum in the Lower Eocene is less pronounced in the generic data set than in the species compilation. Family diversification is muted throughout much of the Phanerozoic. Nonetheless, the Triassic decrease in diversity (from ten families in the Upper Carboniferous to six

families in the Middle Triassic) occurs in both the species and generic plots.

What then is the appropriate taxonomic level for gauging long-term patterns in diversification? Large-scale changes in tracheophyte diversification at the species and family levels are poorly correlated (Fig. 1). This is not surprising given the diversity of lineages that comprise the tracheophytes. The diversification of tracheophyte species may show episodes of increase due to the radiation of a few families even if the majority of the remaining families dwindle in species numbers or go to extinction. Even for a particular group of plants, such as the ferns, there appears to be only a loose correlation between changes over geologic time in species or genus and family numbers, presumably for much the same reason—"taxonomic stacking."

The family may not be the appropriate taxonomic level for analysis for many types of evolutionary questions, as, for example, the identification of mass-extinction events (see next section). A family is eliminated from the fossil record with the extinction of its last surviving species. This terminal extinction event may occur well after the major period of species-attrition within a family. Thus, there

is a double-edged effect in the use of higher taxa for determining unusual perturbations in overall diversity. A "mass-extinction event" may be due to the geologically synchronous elimination of the relic species of numerous, species-depauperate families. On the other hand, many species-rich families could undergo a geologically sudden and severe depauperation in species without the total disappearance of these families from the fossil record. A dramatic reduction in taxonomic diversity below the family level would reflect a significant event in the history of life that could go undetected in family tabulations of diversity. Similar arguments could be made concerning the effectiveness of genus tabulations in detecting intense episodes of species extinction.

Species compilations comprise the most biologically relevant database for paleontology. However, a paleospecies is not operationally defined or identified at the same level of taxonomic scrutiny or with the same body of information and experimental format as a species of living organism. This severely limits the application of conventional species concepts to fossil material.

Recognition of a fossil plant species is perhaps even more difficult than that of a fossil animal species. Plants are phenotypically more plastic than many major groups of animals (Cahn & Harper, 1976; Harper & Bell, 1979; Harper, 1985; White, 1979). The recognition of ecotypes or taxonomic varieties of living plants is notoriously difficult and requires detailed transplant experiments, cytological and electrophoretic examination, and field observations of population dynamics across environmental gradients (Harper, 1977, and references therein). Fossil plants are most frequently found as disarticulated organs which, for many plants, have been previously assigned to separate taxa (Knoll & Rothwell, 1981; Stewart, 1983). Only when found in organic connection can organ genera be placed in synonymy. Consequently, the recognition of genus as an "organ" can only be done on an ad hoc basis. Since whole plant reconstructions are still rare in the paleobo-

tanical literature, the inflation of species richness due to the effects of dealing with fragmented parts is a serious limitation to assessing the true taxonomic diversity in a fossil assemblage.

Perhaps the only reasonable solution to the choice of taxonomic level is to deal with species and genus tabulations for each family. Correlations in the patterns of diversification among all three taxonomic levels for particular groups of plants could then be used to estimate long-term trends or geologically sudden changes in taxonomic richness. As yet this suggested type of multiple-level analysis has not been undertaken for any group of organisms.

MASS EXTINCTIONS: AN ARTIFACT OF HIERARCHY?

Measurements of diversity based on taxa above the species level have been used to determine large-scale evolutionary patterns. Perhaps the best example of this approach comes from the use of family-level data on marine animals to determine major diversification and extinction patterns (Sepkoski, 1980, 1981a, b, 1984; Raup & Sepkoski, 1982, 1984). Sepkoski (1981a, b, 1984, and elsewhere) has argued that family data represent a good proxy for estimating diversity of species (cf. Sepkoski et al., 1981). In addition, comprehensive data with good stratigraphic resolution do not exist for marine animal species or even genera (e.g., Sepkoski, 1984: 247-248). However, as will be shown in this section, the behavior of families as evolutionary "units," and in particular the pattern of family extinction rates, is dependent upon the frequency distribution of species within families.

Raup & Sepkoski (1982, 1984) identified five statistically significant "mass extinction" events in the Phanerozoic record of marine animal families: late Ordovician (Ashgillian), late Devonian (Frasnian), late Permian (Guadalupian-Dzhulfian), late Triassic (Norian), and late Cretaceous (Maastrichtian). Although the magnitudes of species-extinctions are hard to

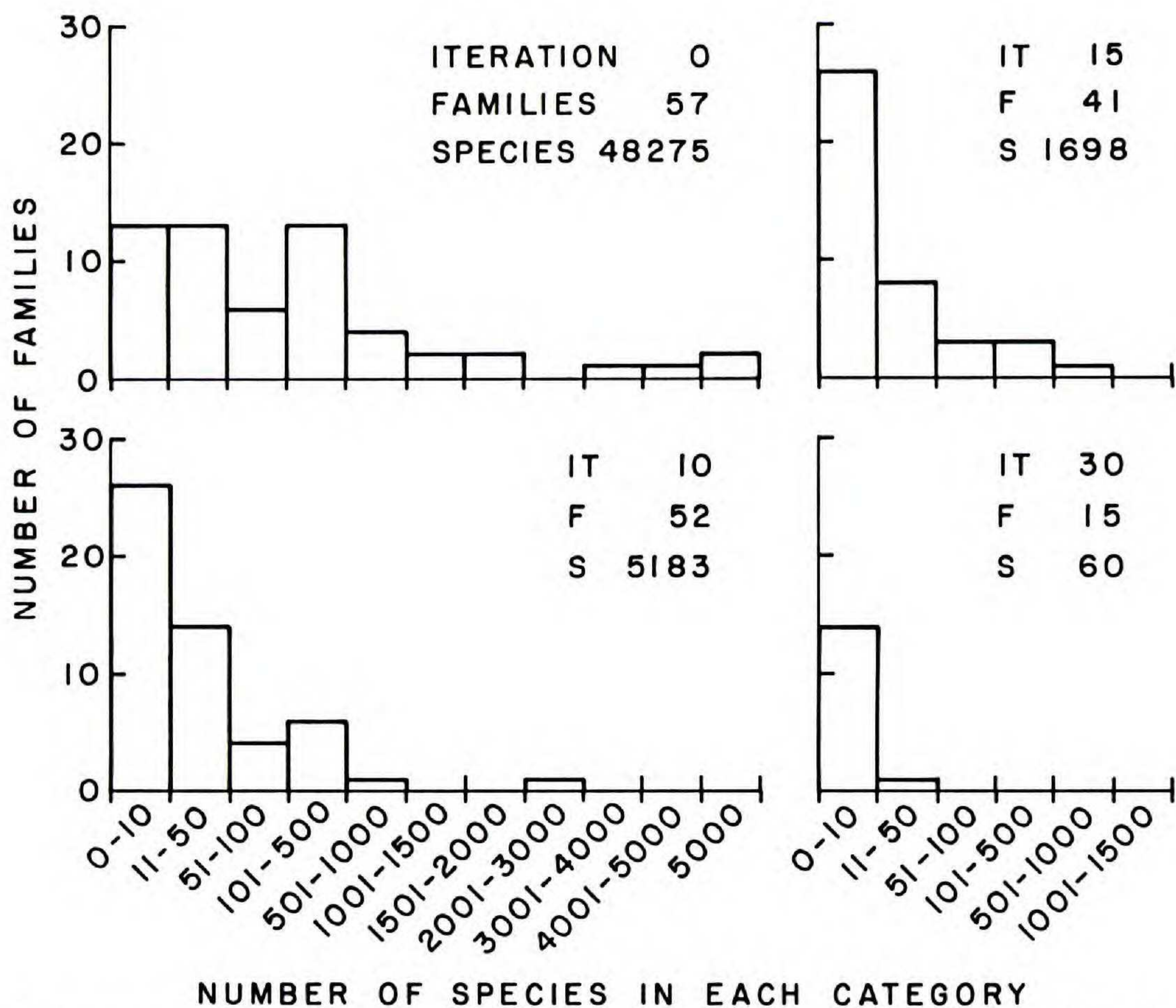


FIGURE 3. Changes in the species frequency distribution of monocotyledon families predicted from a computer simulation of random species extinction. Data from Cronquist (1968, 1981) were used to construct an initial histogram (= iteration 0) representing 57 families and 48,275 species. Random species extinction (20% reduction of species number every iteration) results in a "mass species-extinction event" at iteration 1. Sequential extinction events (which withdraw fewer and fewer absolute numbers of species with each successive iteration) result in shifts of the histogram (cf. Figs. 5, 6).

estimate from the family data, Raup (1979) suggested that the late Permian "mass extinction" event involved a reduction of as many as 96% of marine animal species. Significantly, Raup's regression of family background extinction rates against time yields a negative slope (a long-term decline in family extinction rates), which Raup & Sepkoski (1982) interpreted as reflecting a "fitness-optimization" in which surviving marine taxa become more resistant to extinction through geologic time (but see Kitchell & Pena, 1984). More recently, Sepkoski (1984) modeled the total rate of background extinction (with constant extinction parameters) and suggested that the decline in rates resulted from differential expansion and replacement of evolutionary faunas. Sepkoski's model involves lag phases in the evolutionary behavior of clades within each evolutionary fauna.

A continuous and constant rate of species

extinction can produce discontinuous and abrupt increases in rates of family extinction provided blocks of species go to extinction. This can be illustrated by modeling family extinction rates based on the species frequency distributions of angiosperms.

Data on the approximate numbers of species per family in the major groups of angiosperms are provided by Cronquist (1968, 1981). Histograms of the species frequency distributions in the families of monocotyledons and dicotyledons are shown in Figures 3 and 4. In both cases, the majority of families have fewer than 500 species per family; however, both monocots and dicots have families with species numbers in excess of 5,000. (The Compositae with 19,000 species is not shown in the data set for dicotyledons.) These distributions are similar to those constructed by Clayton (1972, 1974) for the generic frequency distribution in angiosperm families, which conforms to a

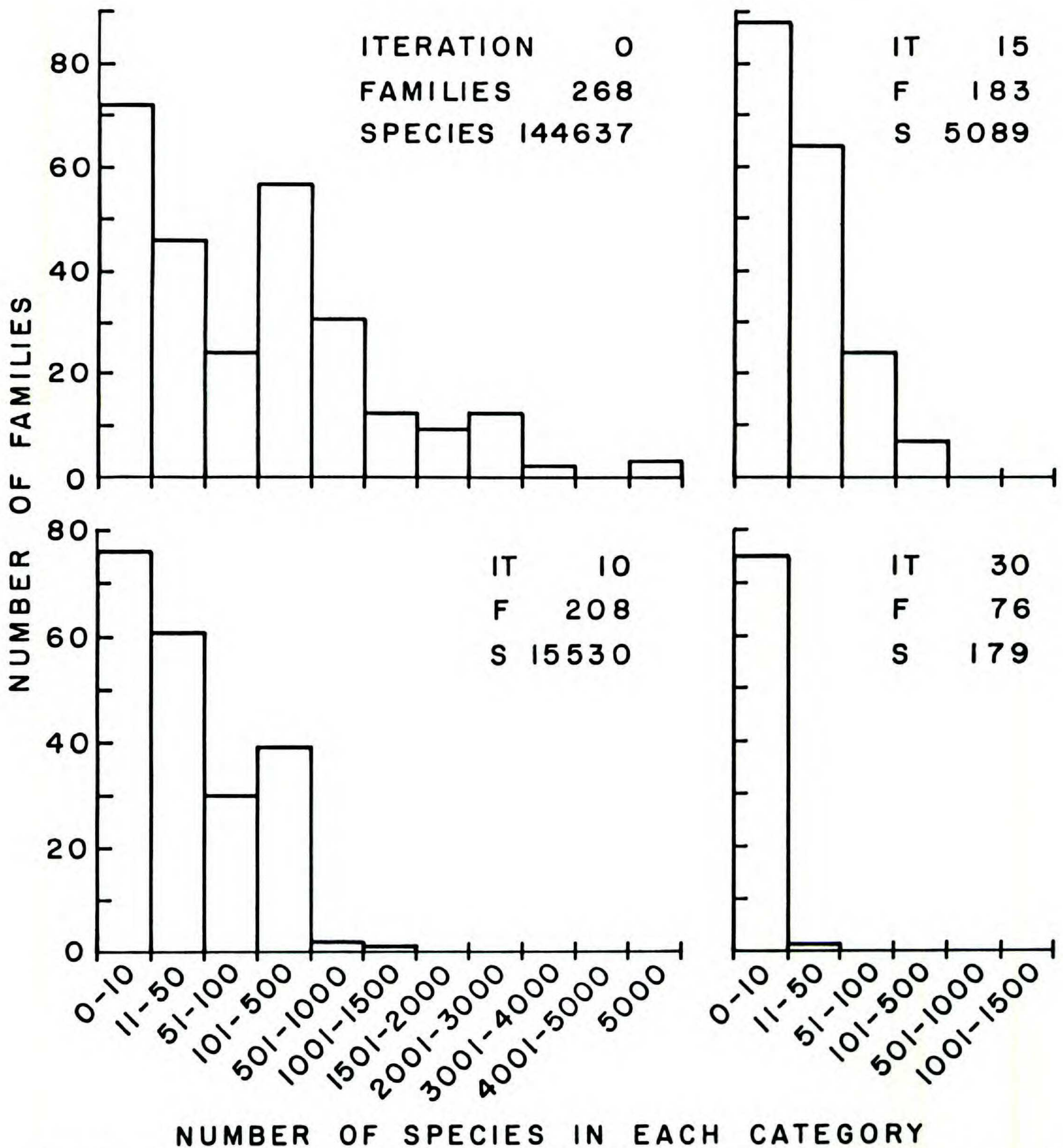


FIGURE 4. Changes in the species frequency distribution in dicotyledon families predicted from a computer simulation of random species extinction. Data from Cronquist (1968) were used to construct the initial histogram (= iteration 0) representing 268 dicot families and 144,637 species (the Compositae are not included in this simulation). Random species extinction (20% reduction in number of species every iteration) results in a "mass species-extinction event" at iteration 1. Sequential extinction events result in the reduction of dicotyledon families (cf. Figs. 5, 6).

logarithmic distribution. Consequently, the following arguments against the use of family compilations for determining mass extinction events can be extended to the use of genus tabulations.

A computer simulation technique was de-

vised to track the family extinction rate as a constant percentage of species is reiteratively removed from each clade. The species undergoing extinction were selected randomly among all families by means of the standard linear congruent method, which does not bias

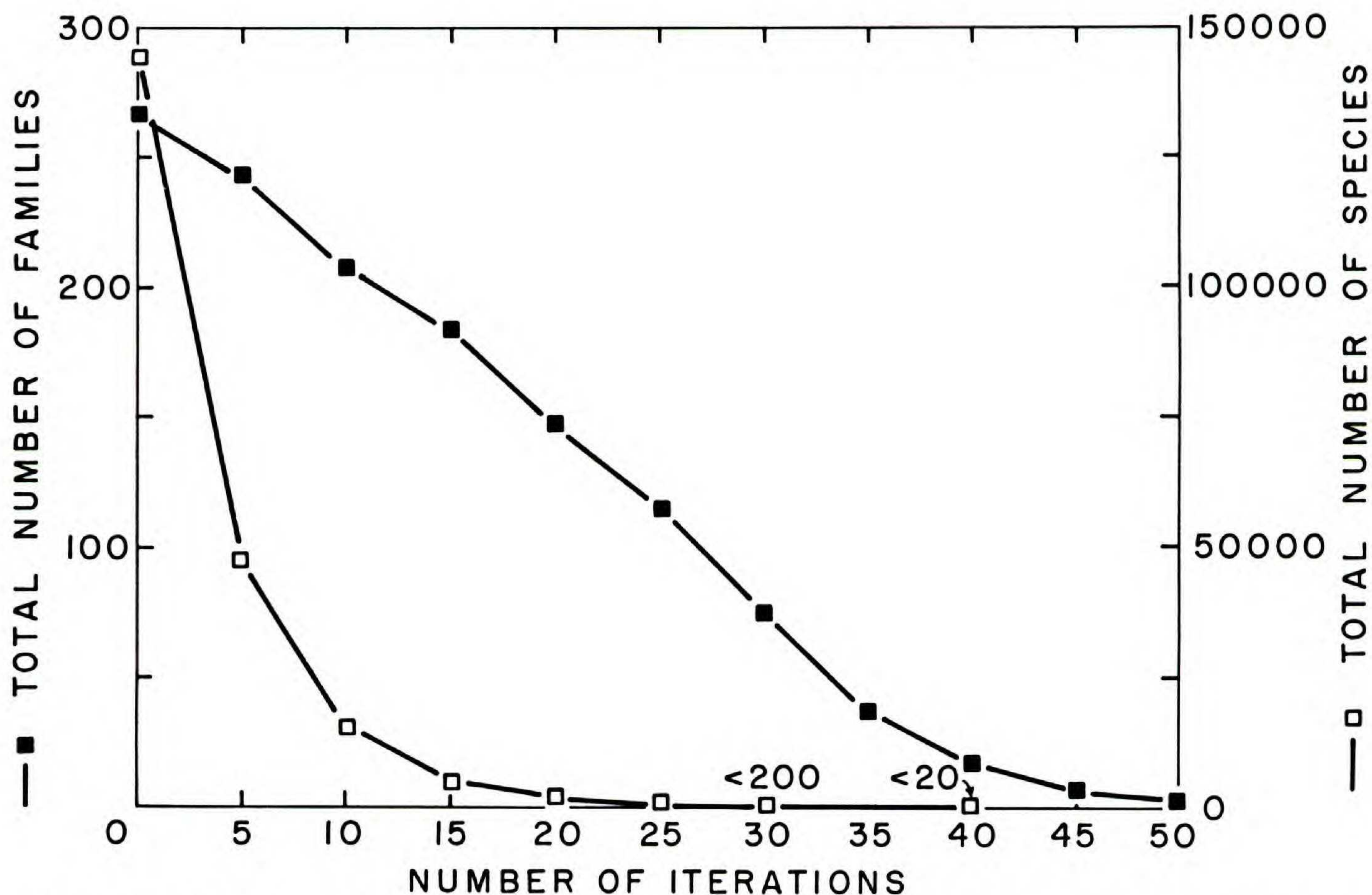


FIGURE 5. Changes in the total number of dicotyledon species and families over 50 iterations of species extinction (20% reduction in number of species every iteration). Numbers of species decline exponentially; numbers of families decline in as near linear function until the 35th iteration.

the probability of species extinction toward large or small families. Consequently, all species have an equal probability of going to extinction. If a constant percentage of species goes to extinction, then a "mass-species" extinction event occurs on the first iterative cycle of each simulation, i.e., each simulation starts out with the maximum number of species; therefore, the first cadre of species to go to extinction is the largest in absolute number. Successive extinction events result in a progressive decline in the absolute number of species undergoing extinction. The use of a constant percentage extinction rate provides an opportunity to look for possible correlations between mass-species and mass-family extinction events. Simulations in which a constant number of species go extinct ($ds/dt = k$) rather than a constant percentage of species yield similar patterns of family extinction but require extended reiterative cycles of species extinction. Each simulation based on a constant-percentage rate of species ex-

inction was run for 50 reiterative cycles. At this point most families (99%) became extinct.

The consequences of successive iterative species extinctions on the frequency distributions of monocot and dicot families is shown in Figures 3–5. As expected, each histogram gradually shifts toward the left (= numerous species-poor families). Figure 5 shows that species numbers exponentially decrease and asymptotically approach the x -axis (which is a very crude analogue to time, since there is no a priori way to relate an iteration of species extinction to an interval of geologic time); decrease in the number of families with successive iterative species extinctions is nearly linear. Various species-extinction rates ranging from 10% to 50% yield comparable patterns. Significantly, however, total family-extinction rates (number of families going to extinction per iteration) are not constant. Comparisons between the dicot and monocot simulations are shown in Figure 6. The total family-extinction rate, E_F , for dicots increases

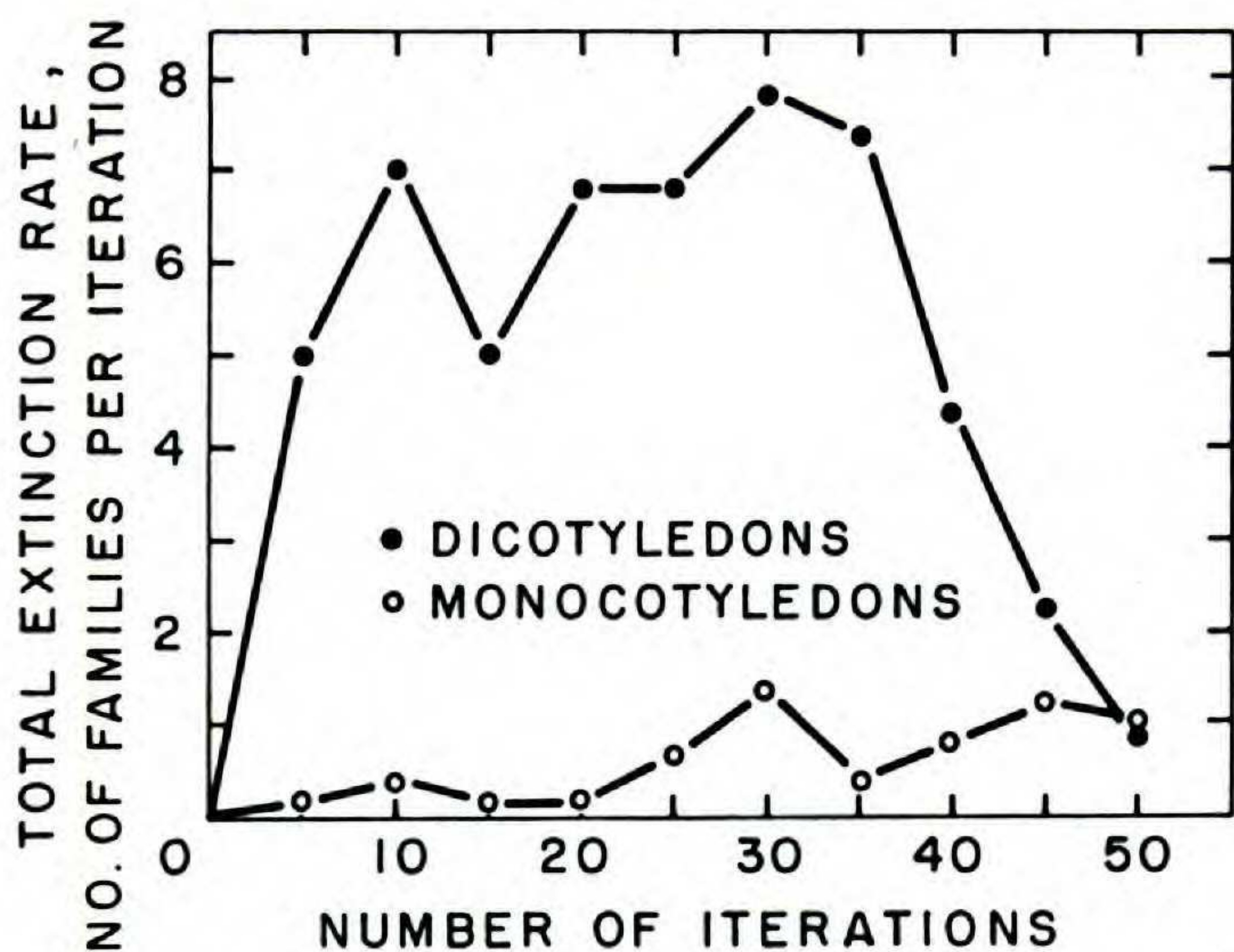


FIGURE 6. Patterns of the total extinction rate of dicotyledon and monocotyledon families resulting from a 20% species-extinction rate. These values were computed on the basis of data shown in Figure 5.

sharply to 7.0 (after 10 iterations), decreases to 5.0 (after 15 iterations), and then plateaus before it sharply declines after 35 iterations. A pattern that is qualitatively and quantitatively dissimilar to dicots is observed for the monocot simulation, e.g., E_f never exceeds 1.4 and increases only slightly over many iterations.

Differences between the patterns of family-extinction rates for monocots and dicots are due solely to differences in their respective initial species frequency distribution in families. To test the sensitivity of patterns of family-extinction rates to the frequency distribution of species among families, three artificial distributions were created: (1) one in which the majority of families contains many species (skewed to the right); (2) a distribution having an equal number of families in each category of species-richness (= horizontal distribution); and (3) one in which the majority of families contains few species (= the frequency distribution is skewed to the left). In each case, the total number of families was held constant ($N = 111$). Owing to the nature of the distributive functions, the total numbers of species and families in each distribution cannot be equal in each of the three cases. However, species-extinction rates are based on percentages, and family-extinction rates are the subject of concern. Therefore, the inequality of species numbers in the three

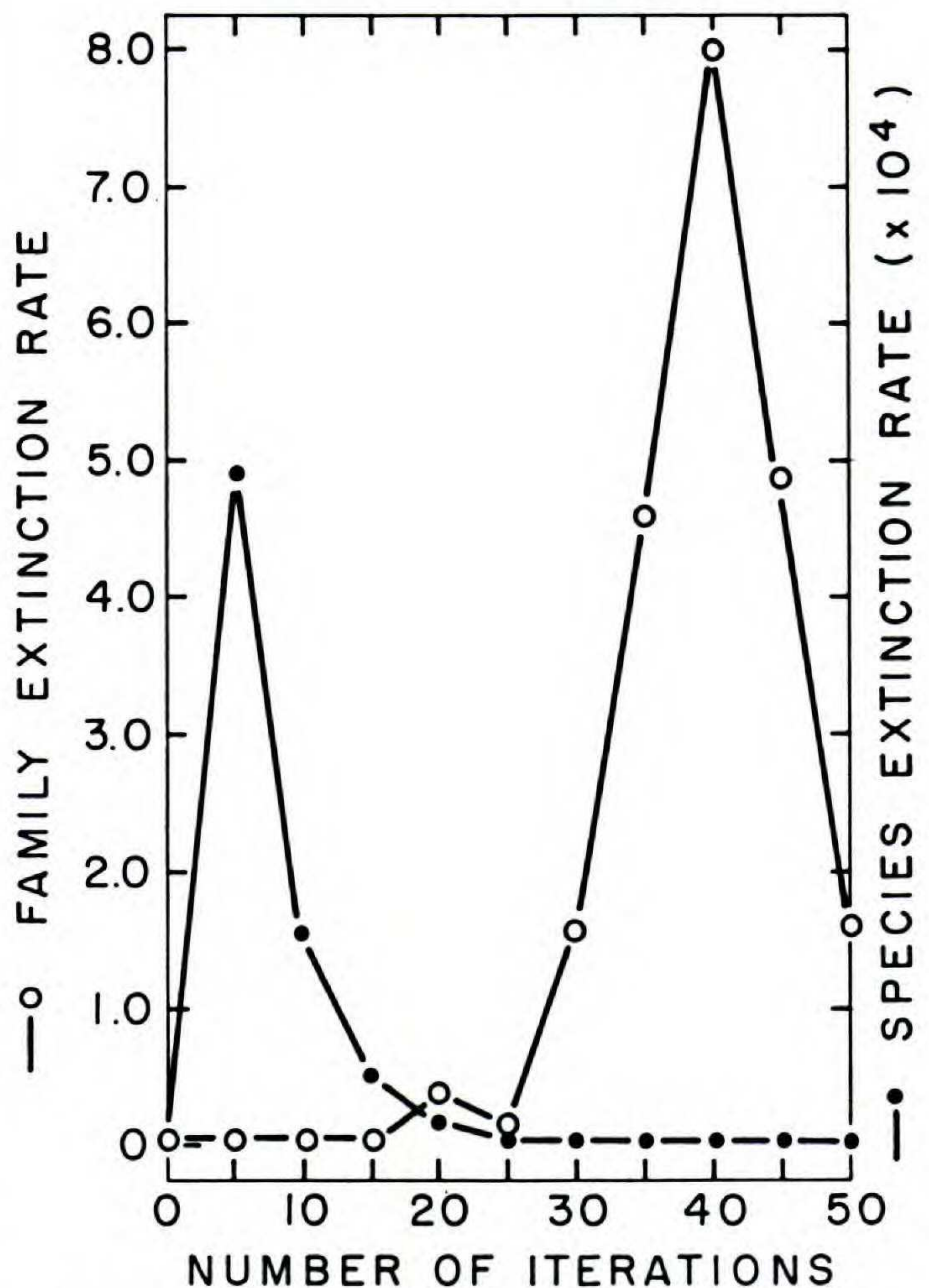


FIGURE 7. Patterns of the total extinction rate computed for an artificially constructed species frequency distribution in which many families are species-rich and only a few families are species-poor. The total number of families in this simulation is 111; the total number of species is 360,871. A "mass species-extinction event" is apparent by the fifth iteration of 20% species extinction. The largest absolute number of species to go extinct occurs at the first iteration. However, data are graphed showing the summation of extinction events for intervals of five iterations. This is necessary because family extinction rates per iteration are very low. A "mass family-extinction event" is simulated at the 40th iteration.

frequency distributions does not appreciably influence comparisons among the three trends in family extinctions.

Figures 7–9 show the resulting patterns of total family-extinction rates for the three artificially created frequency distributions. A greater resolution of these peaks (in which family-extinction events are plotted every iteration) is possible. However, the number of families eliminated per iteration is very small (1–3 families); therefore, the magnitude of peaks in family-extinction rates would be small (1–3 families per iteration). By calculating family-extinction rates every five iterations,

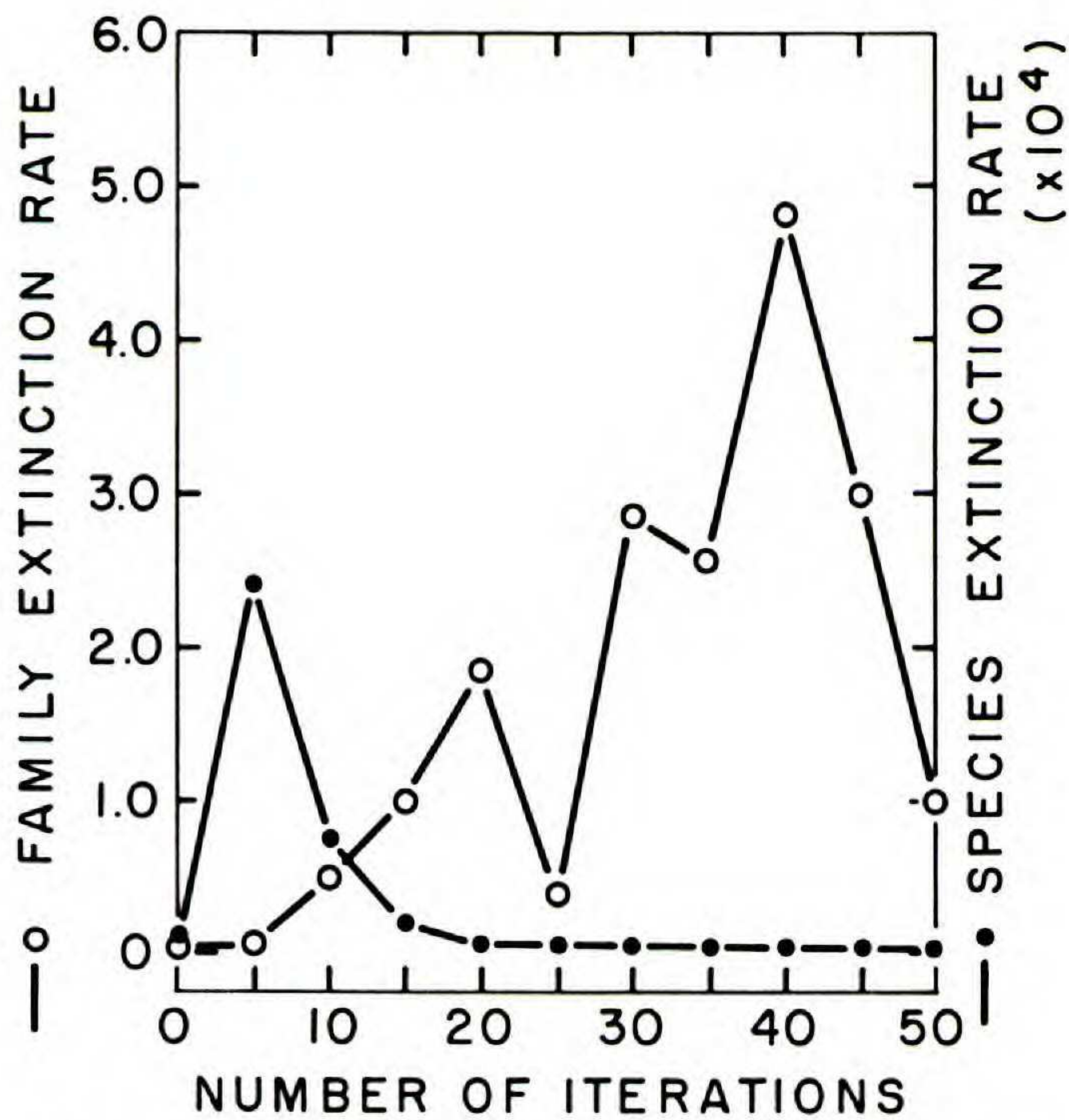


FIGURE 8. Patterns of the total extinction rate computed for an artificially constructed species frequency distribution in which all categories of species richness are occupied by equivalent numbers of families ($N = 111$). The total number of species is 176,600. This species frequency distribution produces a "spiked" pattern of total family-extinction rate with a 20% species-extinction rate.

the pattern of family extinctions is emphasized. The distribution skewed to the right (= most families with many species) shows a pattern vaguely reminiscent of a "mass extinction," in which the rate of family extinction varies little about a mean value of 0.12 through 25 iterations and then sharply increases to 8.0 after 40 iterations before declining to 1.6 at 50 iterations (Fig. 7). The pattern of extinction occurring up to 25 iterations results from the gradual and random extinction of a few species-depauperate families. With each successive iteration, however, species-rich families are reduced in numbers of species but, due to their large initial sizes, fail to go to extinction. After 25 iterations the "species buffering" experienced by these families is eroded and they become sufficiently depleted such that they collectively undergo a "mass family extinction." Only 2.7% of the total number of families are eliminated by the 25th iteration despite the extinction of over 99.5% of the original number of species. If this simulation reflected a real case from the fossil record, an abrupt increase in the rate

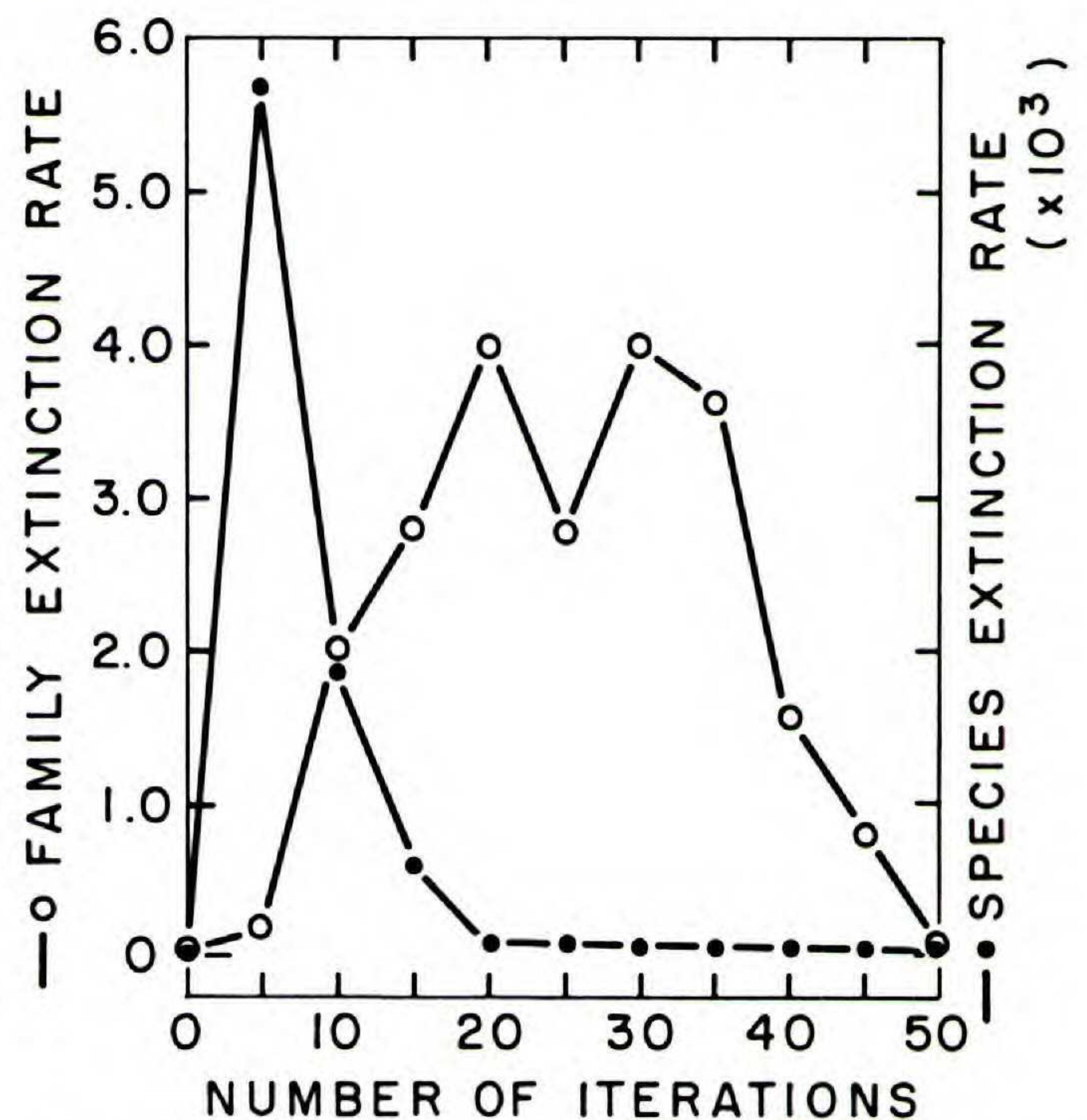


FIGURE 9. Patterns of the total extinction rate computed for a species frequency distribution with many species-poor families and a few species-rich families ($N = 111$). A total of 43,070 species are represented in this artificially created distribution.

of family extinction would not coincide with a mass species-extinction event: by the 15th iteration, over 96% of all species are eliminated, despite the survival of all families.

Similar incongruities between the extent to which family extinctions reflect or coincide with species extinctions are seen in the other two simulations. An even distribution in the number of families containing the various categories of species numbers produces an ascending but spiked pattern of family-extinction rates (Fig. 8). A distribution skewed toward many species-poor families yields a broad, irregularly plateaued pattern of family-extinction rates, which is somewhat similar to the pattern generated from the dicot data set (Fig. 9). These two frequency distributions are clearly artificial since neither is encountered in real species, genus, or family tabulations. Nonetheless, they are of interest because they indicate that no frequency distribution produces a correlation between species- and family-extinction patterns.

Computer simulations do not indicate that family-level compilations are necessarily inadequate to gauge "mass extinction" events. Clearly, there is no reason to assume that

species extinctions are randomly distributed among all families. However, (1) "spikes" in the regression of family-extinction rates against geologic time can reflect the synchronous demise of many species-poor families belonging to a once robust taxonomic (or grade-level) cohort; (2) patterns in family-extinction rates are dependent upon the frequency distribution of species among the families considered; (3) mass species-extinction and mass family-extinction events may not coincide; indeed, the vast majority of species within a clade may disappear well before the event is noticeable at the family level (as in the case of *Ginkgo*); and (4) analyses of mass extinctions require information on the changing patterns of species distributions within suprageneric taxa. Similar arguments can be made for the use of generic tabulations to detect mass-extinction events (cf. Raup & Sepkoski, 1986; see also Hoffman, 1986). Similarly, diversity measured solely on the basis of species numbers ignores the relative abundance of individuals within taxa—an essential feature to understanding the ecological significance of an extinction event. The "mass extinction" of many species that contribute only a fraction of the biomass to a biota has a decidedly different effect than one involving species contributing many individuals to a biota.

NONTAXONOMIC MEASUREMENTS OF DIVERSITY

A treatment of diversity strictly from the perspective of changes in species numbers ignores many significant aspects of plant evolution. Qualitative changes in reproductive and vegetative morphology and quantitative changes in the numbers of individuals within a taxon are not reflected in patterns of changing species numbers. For example, the number of gymnosperm species during the Jurassic and Cretaceous remained relatively constant despite considerable taxonomic turnover within various lineages and significant alterations in morphology and anatomy of representative species. *Ginkgo biloba*, as a

species, occurs from the Mesozoic to the present, yet the number of individuals significantly declined during the Cenozoic. Clearly, evaluations of diversity based on something other than species numbers are important in evaluating adaptive evolution and changes in community structure (Spicer & Hill, 1979; Phillips & DiMichele, 1981; DiMichele et al., 1985; Fisher, 1985).

Another reason for evaluating nontaxonomic measurements of diversity is that inferences on genomic (hence speciation) rates of evolution based on rates of morphological evolution may be faulty. Schopf et al. (1975) argued that differences in the number of species among lineages can be the consequence of dealing with taxa that differ in their degree of morphological complexity. If fossil species truly represent genomically distinct entities (sensu the biological species concept), then rates of morphological and genomic evolution would be highly correlated. These authors, however, assert that this direct correspondence can never be proven. Therefore, it is advisable to look at rates of morphological evolution and rates of paleospecies origination separately.

Fortunately, changes in species numbers and within-assembly species composition, and morphological patterns of long-term evolution can be dealt with separately to visualize tracheophyte diversification. As in most cases with the use of paleontological data, however, quantitative analyses can only be used to construct qualitative comparisons or generalizations. Among these guarded generalizations are:

- (1) The taxonomic composition of fossil plant assemblages is rarely, if ever, stable. It is altered most significantly by the substitution of taxa within related lineages during periods of relatively constant overall species numbers. These "intrataxonomic" alterations occur over extended geological time-scales and are generally discernable among lineages that share a common mode of sexual reproduction (Knoll, 1986).

TABLE 1. Mean species numbers, \bar{x} , of vascular plants in fossil assemblages for representative intervals.

	Niklas et al., 1980 \bar{x} (number of floras)	Knoll, 1986 \bar{x} (number of floras)
Early Devonian	5 (7)	4.0 (8)
Late Devonian	8.2 (9)	10.7 (7)
Early Mississippian	10 (7)	11.9 (15)
Late Mississippian	22.5 (2)	23.3 (8)
Late Jurassic	27.5 (15)	30.8 (6)
Early Cretaceous	21.5 (15)	30.2 (22)
Late Cretaceous	43 (7)	54.4 (17)

- (2) Global species numbers generally increase most significantly with the radiation of plants sharing a novel mode of sexual reproduction (Niklas et al., 1980, 1985).
- (3) At least within the temporal resolution permitted by most paleontological studies, changes in taxonomic composition and large-scale species numbers are tightly linked to changes in vegetative morphology and the appearance of diverse growth habits (Niklas, 1987).
- (4) The appearance of new reproductive modes and diverse morphologies within a clade or cohort of clades may not necessarily result in the ecological displacement of previously existing species. Throughout much of the Paleozoic and Mesozoic, taxonomic radiations are associated with the exploitation of environments not previously occupied (Tiffney, 1981; Knoll, 1986).
- (5) The competitive advantages conferred upon a taxon by novel reproductive or vegetative capabilities are most pronounced early during its taxonomic radiation (Knoll et al., 1984; Knoll & Niklas, 1987).

Each of these generalities is not without exception or debatable inference, since each is based on a limited number of studies. It is more instructive to review the nature of the data upon which these statements are based and to examine their deficiencies.

To date, only two studies have examined changes in the mean species numbers of plants throughout the Phanerozoic (Niklas et al., 1980; Knoll, 1986). In both cases, fossil assemblages (= "floras") were selected from similar depositional environments so as to minimize the differential effects of sedimentological factors on preservation. The floras were selected from what were inferred to be warm climates. Comparison between the mean species numbers per flora for representative time periods is given in Table 1. Despite differences in the sources of data, both studies reported remarkably similar trends. Mean species numbers within floras have increased significantly at least twice during the last 420 million years—doubling between Late Devonian and Late Mississippian floras, and once again between Early and Late Cretaceous floras. (The lack of an objective baseline comparison for the Late Devonian floras precludes evaluation of the data from Early and Late Devonian floras.)

Each of the two increases in mean species number coincides with an increase in overall species diversity (Niklas et al., 1980, 1985). This is to be expected, since the latter incorporates data used to compile within-floras species numbers. However, each of the two increases in mean species numbers correlates with major transitions in the taxonomic composition of floras. This is shown elegantly in a study by Knoll (1986), who presented a unique analysis of the taxonomic composition of floras throughout the Phanerozoic. Figure 10 (redrawn from Knoll's study) shows two significant resortings of suprageneric groups within floras. One occurs with the advent of seed plants in the Late Devonian and Mississippian; another reflects the radiation of flowering plants in the Cretaceous. If the various plant lineages within Knoll's data set are grouped according to their principal modes of reproduction, then the changes in taxonomic composition are seen more clearly (Fig. 11). As in the plots of large-scale species numbers (Fig. 1), the early Paleozoic floras dominated by pteridophytes are replaced by gymnosperm-dominated Mesozoic floras,

which in turn are replaced by floras dominated by angiosperms.

However, Figure 11 masks the taxonomic restructuring in floras that occurs within each category of reproductive mode. The expansion of gymnosperm species in Mesozoic floras occurs at the expense of pteridophytes made up of lineages that did not fall off at equal rates. In general, the numbers of fern species are much less affected than those of lycopods and sphenopsids. Similarly, gymnosperm lineages undergo a more or less continuous intrataxonomic restructuring.

The evolutionary appearance of novel modes of reproduction, for example, seeds and flowers, is often associated with alterations in growth habit (Tiffney, 1981; Tiffney & Niklas, 1985). The number of plant families characterized by cryptogamic (pteridophytes) and phanerogamic reproduction (gymnosperms and angiosperms), as well as the number of families with principally nonarborescent and arborescent growth forms, are plotted through time in Figure 12. In this figure a number of "cross-overs" are seen which can be related to changes in taxonomic composition. For example, during the Carboniferous and Permian, arborescence rises even though cryptogamic reproduction remains more common. Although seed plant species dominate Mesozoic floras, nonarborescence is more common than arborescence during the Jurassic. During the Cretaceous, the number of phanerogamic plant families gradually increases, until by the Late Cretaceous, arborescent/phanerogamic-dominated floras which persist through the Tertiary are established. The Permo-Triassic is a period of considerable restructuring in both the principal modes of reproduction and growth habits. Before the Triassic, arborescent cryptogamic families are dominant, while during the Triassic nonarborescent phanerogamic families are common.

From a much more comprehensive analysis, Tiffney & Niklas (1985) concluded that the history of clonality in land plants can be segregated into three stages: (1) *Silurian to lower Carboniferous* during which clonal lin-

eages dominated, but in which arborescence appeared as a vegetative correlate with heterospory or the seed habit; (2) *Permo-Triassic to Cretaceous*, in which families of arborescent gymnosperms gradually increased and gained numerical dominance over families of arborescent and nonarborescent pteridophytes; and (3) *Cretaceous to present*, which marks the combination of rhizomatous growth and the seed habit (herbaceous angiosperms) which became increasingly more important in the later Tertiary and Quaternary.

Unfortunately these analyses are based on familial data (whole-plant reconstructions are too few to determine large-scale patterns in the evolution of tracheophyte growth habits). Accordingly they provide few insights into species patterns of growth habit or values of relative abundance. Although nonarborescent families dominate much of the early and middle Mesozoic, the abundance of arborescent gymnosperm species in these floras is much higher than that of pteridophytes (Fig. 10). Clearly the family-diversity plots shown in Figure 12 are not reflective of community structure.

As Schopf et al. (1975) pointed out, it is possible that paleontologists fail to recognize the true diversity of morphologically simple organisms and overestimate the diversity of morphologically complex organisms. Thus, periods of rapid taxonomic diversification may be inherently related to (and possibly the product of) episodes of rapid morphological diversification. New vegetative and reproductive features provide the potential to discriminate new phenetic taxa (= paleospecies). As the number of potential taxonomic characters increases, the number of possible permutations of characters increases exponentially. There is little agreement among specialists as to which feature(s) (anatomy, morphology, reproduction, or even geologic age) contribute(s) to identification of a new species. Certainly among disparate taxonomic groups of plants, species are recognized on often very divergent categories of features: more derived taxa, such as the angiosperms, have more numerous and potentially more complex fea-

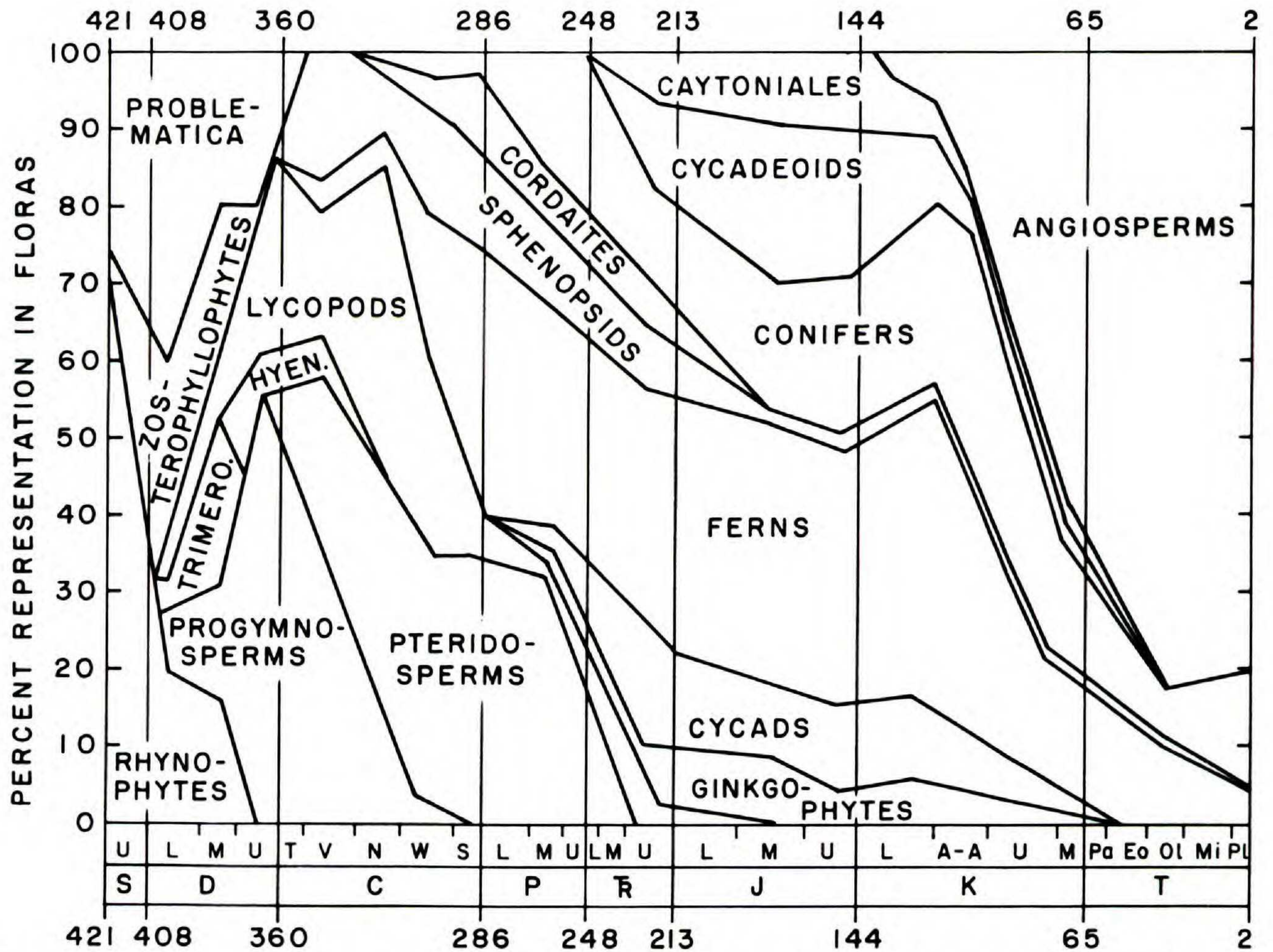


FIGURE 10. Percent taxonomic composition of tracheophytes in fossil assemblages through the Phanerozoic (data redrawn from Knoll, 1986; courtesy of A. H. Knoll). These data show similarities with those presented by Niklas et al. (1985) for overall patterns in diversification within separate lineages of vascular land plants. Early Paleozoic floras were dominated by archaic pteridophytic groups (rhyniophytes, zosterophyllophytes, trimerophytes) which radiated into variously more derived groups during the Carboniferous. Mesozoic floras consist of diverse gymnosperm lineages supplemented by numerous ferns. With the radiation of angiosperms, the percent taxonomic representation of nonflowering groups declines abruptly during the Late Cretaceous and Tertiary.

tures with which to identify species (e.g., floral structure) than more archaic taxa, such as pteridophytes (e.g., stelar anatomy, spore-wall characters).

The Devonian flora provides a convenient illustration of the potential relationship between taxonomic and morphological rates of evolution. There is considerable agreement among specialists as to the features that distinguish Devonian genera and higher taxa. Additionally, there are authoritative treatments of the stratigraphic occurrences of taxa and the first and last occurrences of various vegetative and reproductive features upon which they are based. For example, Chaloner & Sheerin (1979) provided a comprehensive stratigraphic treatment of Devonian genera as well as the first and last occurrences of

various reproductive and vegetative features. Their data are plotted in Figures 13 and 14. (Nonvascular genera, such as *Sporogonites*, *Parka*, *Pachytheca*, or those having dubious status as tracheophytes, such as *Taeniocrada*, are excluded from these plots.) Anatomical (tracheid, stelar, and stomatal type; Chaloner & Sheerin, 1979, figs. 2, 3) features are plotted separately from reproductive features, such as the position, shape, and type of dehiscence of sporangia (Chaloner & Sheerin, 1979, fig. 4). The data indicate that the number of Devonian genera increases from the Pridolian to the Givetian and then undergoes a modest decline in the Frasnian and Famennian (Fig. 13). By contrast, the number of vegetative and reproductive features upon which Devonian taxa are based increases

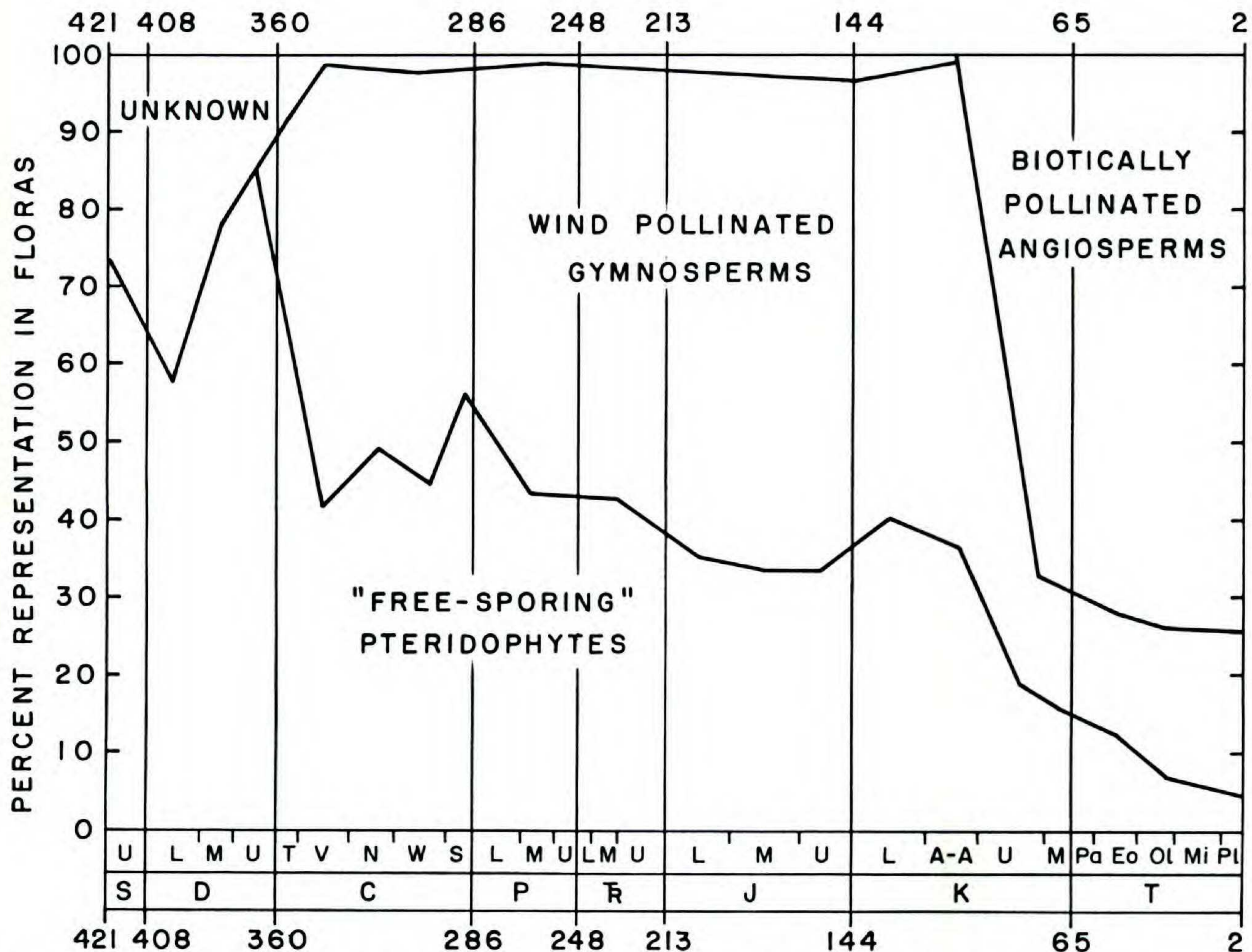


FIGURE 11. Percent taxonomic composition of tracheophytes (shown in Fig. 10) converted to represent major categories of sexual reproduction. Free-sporing pteridophytes dominate most of the early Paleozoic floras; gymnosperms predominate through most of the Mesozoic; and angiosperms dominate the Late Cretaceous and Tertiary.

throughout this interval. Linear regression analysis of the total number of taxonomic characters versus the number of genera yields $r = 0.96$ ($N = 8$), which is significant at the 1% level. This correlation, however, reveals very little with regard to the quantitative decrease in Late Devonian genera despite an increase in the potential number of taxonomic characters in the Frasnian-Famennian. Clearly, as the number of genera increases it is reasonable to expect an increase in the number of taxonomically distinguishable features. Analyses of the appearance of new genera and of new vegetative/reproductive features yield poor correlations (Fig. 14). For example, a regression of the number of new genera against that of the number of reproductive features yields $r = 0.283$. Regressions of either the number of vegetative or the total number of features against the number of Devonian genera yield lower coefficients of

correlation. Consequently, the taxonomic recognition of new Devonian genera does not appear to be correlated necessarily with the evolutionary appearance of novel reproductive or vegetative features. In addition, a review of the generic descriptions for Devonian vascular plants compiled by Gensel & Andrews (1984) suggests that paleobotanical treatments of early Paleozoic floras are taxonomically conservative. Therefore, at least at the generic level, it does not appear that estimates of taxonomic diversification in the Devonian are artifacts of rapid morphological evolution. Since most Devonian genera have few species, this conclusion appears warranted at the species level as well (cf. Knoll et al., 1984).

Although the perceived taxonomic diversification of early vascular land plants appears not to be biased by rapid morphological evolution, other episodes of large-scale increases

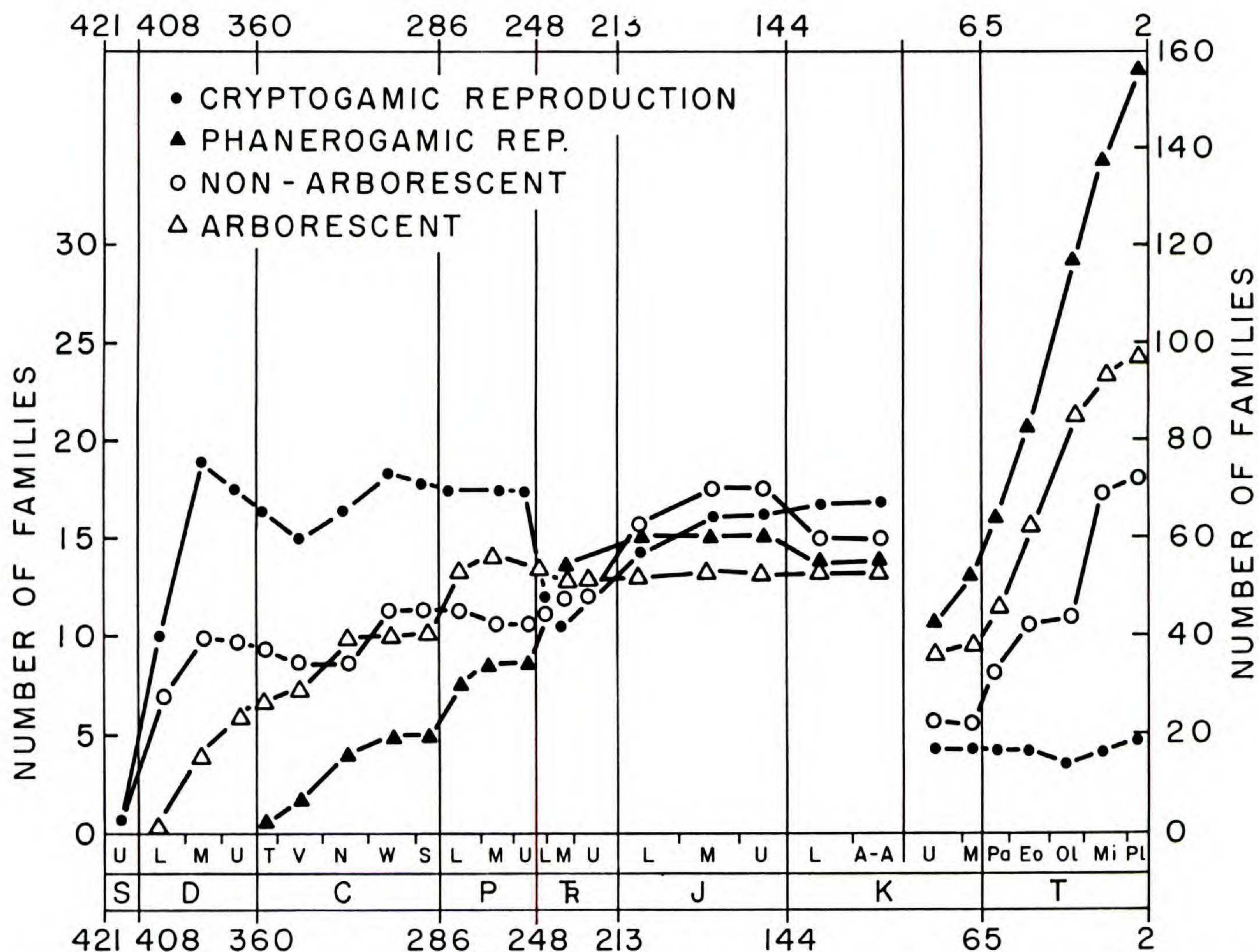


FIGURE 12. Absolute numbers of spore- and seed-bearing, nonarborescent and arborescent tracheophyte families through the Phanerozoic (redrawn from Tiffney & Niklas, 1985). The scale of the vertical axis changes from increments of five families to increments of 20 between the Lower and Upper Cretaceous.

in numbers of species have not been rigorously examined. For philosophical and practical reasons, therefore, it is reasonable to view conservatively the overall patterns of tracheophyte species diversification in terms of anatomical, morphological, and reproductive evolutionary trends, rather than strictly in the context of patterns of species origination.

NULL OR BIOLOGICAL HYPOTHESES?

Historically, evolutionary theory has come almost exclusively from observations made on living organisms. Charles Darwin was able to use the fossil record as evidence for evolution but derived his notion of natural selection from insights gained from animal and plant breeding, biogeography, and natural history. Indeed, he found the fossil record singularly intractable in supporting many features of his

theory (Rudwick, 1976). The Modern Synthesis incorporated paleontology, but even the work of George Gaylord Simpson may be viewed as an ad hoc rationalization of patterns seen in the fossil record based on neontologically derived theory (cf. Gould, 1980). Recently, however, paleontology has generated evolutionary hypotheses based on patterns seen in the fossil record. This significant shift in the source of evolutionary speculation has had many effects, not the least of which is a re-evaluation of the biases, artifacts, and limitations that are inherent to paleontological data. Clearly, the fossil record can be used to generate evolutionary hypotheses, but only provided it reasonably reflects biological phenomena. For a long time paleontologists have recognized the numerous geological factors that contrive to filter and distort biological processes preserved in the record. Much of the recent literature focuses on attempts to

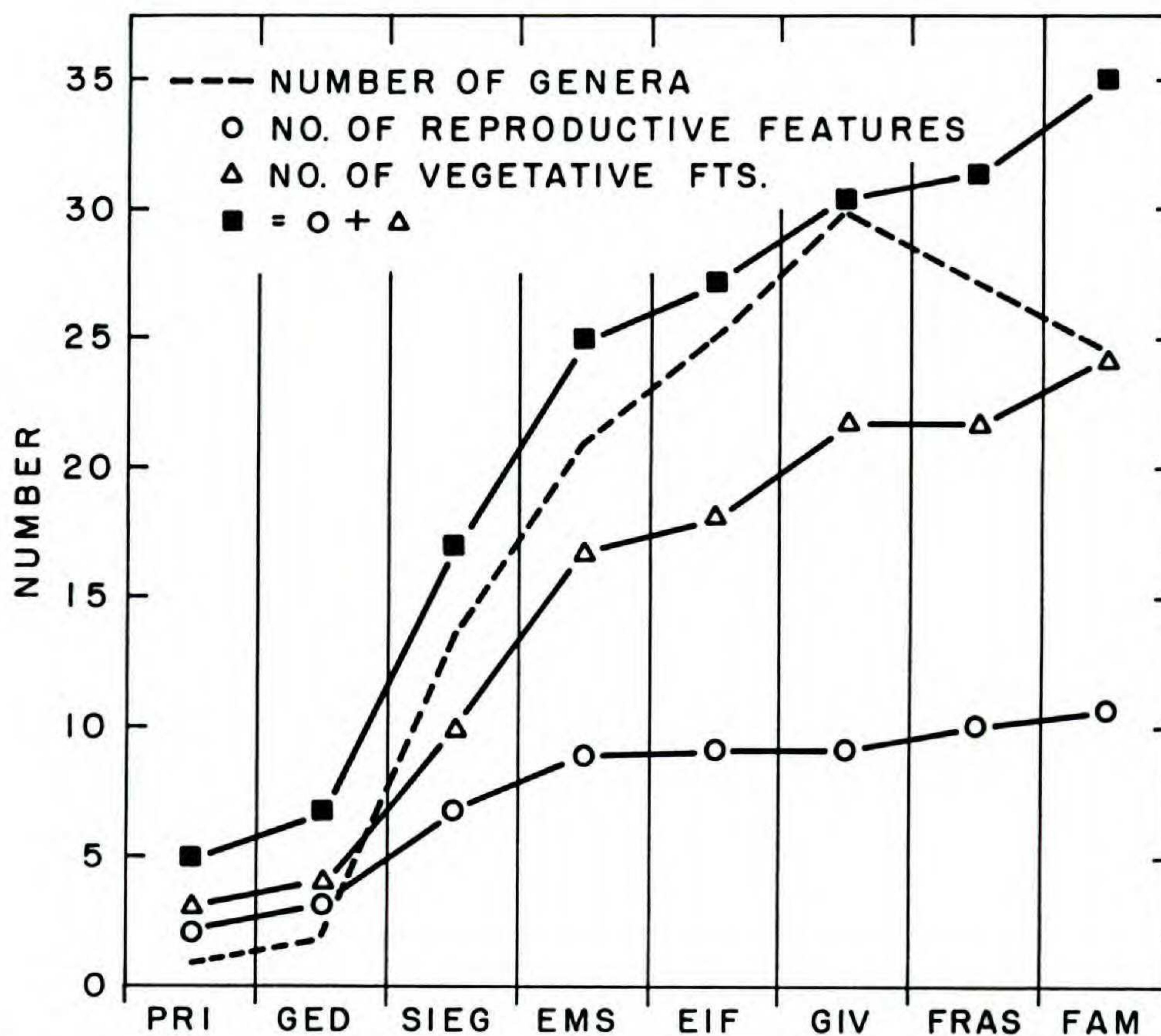


FIGURE 13. Changes in the total number of Devonian vascular plant genera and the number of reproductive and vegetative characters used to identify taxa. Data taken from Chaloner & Sheerin (1979, figs. 1-4). Devonian genera are exclusive of nonvascular and dubiously vascular plants (e.g., *Parka*, *Pachytheca*, *Taeniocrada*, *Prototaxites*, *Sporogonites*, *Spongiophyton*, *Protosalvinia*): Pri = Pridolian, Ged = Gedinnian, Sieg = Siegenian, Ems = Emsian, Eif = Eifelian, Giv = Givetian, Fras = Frasnian, Fam = Famennian.

deal with these factors and to reconstruct information lost from the fossil record (Nichols & Pollock, 1983).

The fossil record is the principal source of information on long-term patterns of evolution. Retained within it are imperfect records of taxonomic diversification, major episodes of adaptive radiations, and major extinctions. This paper has focused on the quality of these patterns for vascular land plants. Quantitative analyses of the paleobotanical literature provide a basis for reconstructing the broad patterns of floristic and vegetational change occurring over the last 400 million years. In particular, large-scale patterns in numbers of species have been used to reconstruct and identify two major floristic changes, one at the end of the Paleozoic and another toward the end of the Mesozoic; within-assemblage taxonomic compositions have been used to treat broad patterns in vascular plant ecology; and morphological/anatomical data have been used to reconstruct trends in organography and adaptation. As has been seen, however,

potentially serious limitations and distortions exist in the data. In almost all cases, quantitative analyses can be used comfortably only to draw qualitative conclusions.

The most serious difficulty with the fossil record comes from attempts to infer mechanisms from patterns. Ecologists are currently debating the use of patterns as data, as the recent furor over the use of null models attests (Harvey et al., 1983). Is there a null hypothesis for the pattern of species diversification seen in the fossil record? The answer is an equivocal yes. The fossil record of land plants exists because of processes of non-marine clastic and pyroclastic deposition. The vast majority of fossil plants are preserved in lowland flood plain or lakeside environments or are entombed in volcanic ashfalls and mudflows. Consequently, it is conceivable and even probable that much of the patterns seen in tracheophyte species diversification can be explained in terms of factors that influence patterns of nonmarine sedimentation. Principal among these is tectonics, which controls

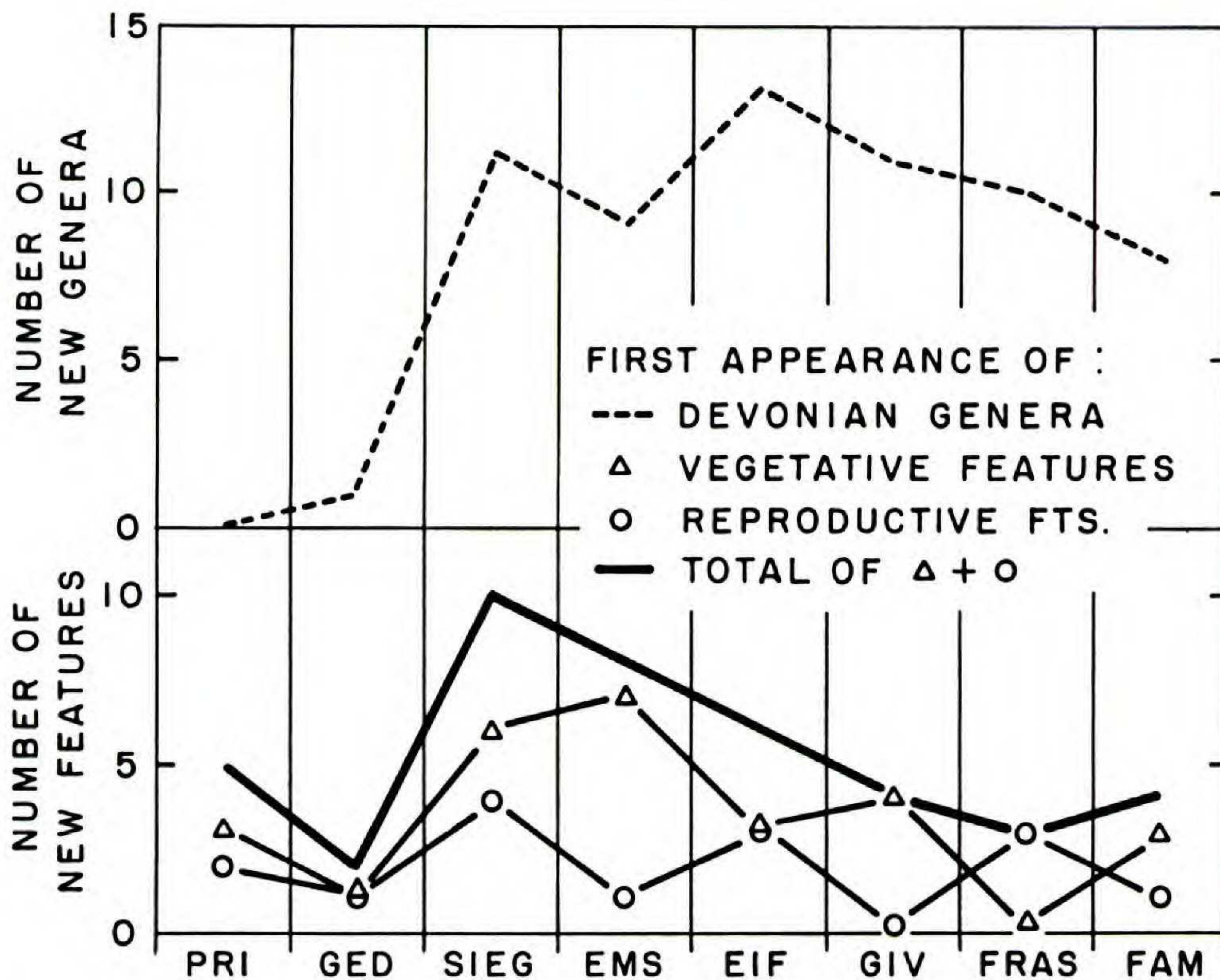


FIGURE 14. Numbers of first appearances of Devonian genera, and vegetative and reproductive features. Data from Chaloner & Sheerin (1979, figs. 2-4).

rates of uplift, erosion, subsidence of sediment-accumulating basins, and volcanism (Blatt et al., 1972).

For example, variation in the type of non-marine sediments deposited during a geologic period could contribute to the apparent pattern of species diversification. Are periods of high numbers of species also those in which geological factors favored the deposition of sediments in which fossils are easily recovered? Fossil plants are preserved most often and with high morphological fidelity in fine-grained carbonaceous detrital sediments and volcanic ash deposits. Niklas et al. (1980) attempted a limited analysis of data on coal resources to estimate coarsely the variation in nonmarine carbonaceous sediments through the Phanerozoic. We concluded that the Carboniferous, Cretaceous, and Tertiary were qualitatively different from other geologic periods. These three "coal eras" have large coal tonnages *per unit of outcrop area*. High numbers of species for these three coal-rich eras could reflect a combination of extensive sedimentological "sampling" of terrestrial floras, excellent preservation (e.g., coal ball petrifications), and the consequence of intensive eco-

nomic exploration of coal resources. These factors probably account for the unusually high numbers of species reported for the Carboniferous and Cretaceous-Tertiary.

Therefore, it is safe to assume that tectonics and erosional patterns of deposition have contributed to the fluctuation in numbers of species in substantial ways. Nonetheless, these nonbiological or null hypotheses are inadequate to explain the patterns of taxonomic turnover within fossil assemblages or broad patterns in plant organographic/reproductive evolution. Regardless of the quantity of sediment deposited or the preservational status of plant parts recorded for a geologic period, there exists no necessary and sufficient correlation between the magnitude and direction of physical factors operating in the fossil record and patterns in taxonomic turnover and morphological evolution. Patterns in plant fossil record can be viewed either from the perspective of "objects" (taxa and their origination, persistence, and extinction) or "properties" (morphological and reproductive innovations and elaborations). A strictly exclusive treatment of either perspective is unlikely to lead to any insights into

the relationship between evolutionary patterns and mechanisms (Sober, 1985). Null hypotheses are an essential component to this type of inquiry, but the assessment of alternative hypotheses and multiple-causation in paleontology requires both geological and biological insights.

The salient conclusions that emerge from a review of the plant fossil record can be briefly summarized under five points. (1) The concepts of a paleospecies and an extant species are significantly different (see Gingerich, 1985). (2) Consequently, the fossil record of species diversification is best viewed as a document of trends in morphological/reproductive diversification. Quantitative estimates of "diversity" can be used to draw primarily qualitative conclusions. (3) The taxonomic richness recorded for any geologic period does not provide information on species equitability, which is an essential component to considerations of paleoecology and the ramifications of phenomena such as extinction. (4) Although the properties of taxa above the level of species are potentially interesting, they do not necessarily reflect those of species, which are the primary focus of evolutionary mechanisms. Finally, (5) much of the pattern of taxonomic diversification could be explained by factors operating in a strictly geological context; however, identification of long-term patterns in biological phenomena requires the examination of trends in morphology, anatomy, and reproductive systems, in conjunction with patterns of species diversification (Raup, 1983).

LITERATURE CITED

- BENTON, M. J. 1985. Patterns in the diversification of Mesozoic non-marine tetrapods and problems in historical diversity analysis. Special Pap. Palaeontol. 33: 185-202.
- BLATT, H., G. MIDDLETON & R. MURRAY. 1972. Origin of Sedimentary Rocks. Prentice-Hall, Englewood Cliffs, New Jersey.
- BOUREAU, E. (editor). 1970. Traite de Paleobotanique, Volume IV (authored by H. N. Andrews, C. A. Arnold, E. Boureau, J. Doubinger & S. Leclercq). Masson et C^e, Paris.
- CAHN, M. & J. L. HARPER. 1976. The biology of the leaf mark polymorphism in *Trifolium repens* L. I. Distribution of phenotypes on a local scale. Heredity 37: 309-325.
- CHALONER, W. G. & A. SHEERIN. 1979. Devonian macrofloras. Special Pap. Palaeontol. 23: 145-161.
- CLAYTON, W. D. 1972. Some aspects of the genus concept. Kew Bull. 27: 281-287.
- . 1974. The logarithmic distribution of angiosperm families. Kew Bull. 29: 271-279.
- CRONQUIST, A. 1968. The Evolution and Classification of Flowering Plants. Houghton Mifflin Co., Boston.
- . 1981. An Integrated System of Classification of Flowering Plants. Columbia Univ. Press, New York.
- DIMICHELE, W. A., T. L. PHILLIPS & R. A. PEPPERS. 1985. The influence of climate and depositional environment on the distribution and evolution of Pennsylvanian coal-swamp plants. Pp. 223-256 in B. H. Tiffney (editor), Geological Factors and the Evolution of Plants. Yale Univ. Press, New Haven, Connecticut.
- FISHER, D. C. 1985. Evolutionary morphology: beyond the analogous, the anecdotal, and the ad hoc. Paleobiology 11: 120-138.
- GENSEL, P. G. & H. N. ANDREWS. 1984. Plant Life in the Devonian. Praeger Press, New York.
- GINGERICH, P. D. 1985. Species in the fossil record: concepts, trends, and transitions. Paleobiology 11: 27-41.
- GIVNISH, T. J. 1986. Biomechanical constraints on crown geometry in forest herbs. Pp. 525-584 in T. J. Givnish (editor), On the Economy of Plant Form and Function. Cambridge Univ. Press, Cambridge.
- GOULD, S. J. 1980. G. G. Simpson, paleontology and the modern synthesis. Pp. 152-172 in E. Mayr & W. B. Provine (editors), The Evolutionary Synthesis—Perspectives on the Unification of Biology. Harvard Univ. Press, Cambridge, Massachusetts.
- HARLAND, W. B., A. V. COX, P. G. LLEWELLYN, C. A. G. PICKTON, A. G. SMITH & R. WALTERS. 1982. A Geologic Time Scale. Cambridge Univ. Press, Cambridge.
- HARPER, J. L. 1977. Population Biology of Plants. Academic Press, London.
- . 1985. Modules, branches, and the capture of resources. Pp. 1-34 in J. B. C. Jackson, L. W. Buss & R. E. Cook (editors), Population Biology and Evolution of Clonal Organisms. Yale Univ. Press, New Haven, Connecticut.
- & A. D. BELL. 1979. The population dynamics of growth form in organisms with modular construction. Pp. 29-52 in R. M. Anderson, B. D. Turner & L. R. Taylor (editors), Population Dynamics. Blackwell Press, Oxford.
- HARVEY, P. H., R. H. COLWELL, J. W. SILVERTOWN & R. M. MAY. 1983. Null models in ecology. Ann. Rev. Ecol. Syst. 14: 189-211.
- HOFFMAN, A. 1986. Neutral model of Phanerozoic diversification: implications for macroevolution. N. Jb. Geol. Palaont., Abh. 172: 219-244.
- KIDWELL, S. M. 1986. Models for fossil concentrations: paleobiologic implications. Paleocology 12: 6-24.
- KITCHELL, J. A. & D. PENA. 1984. Periodicity of extinctions in the geologic past: deterministic versus stochastic explanations. Science 226: 689-692.
- KNOLL, A. H. 1984. Patterns of extinction in the fossil record of vascular plants. Pp. 21-68 in M. Nitecki (editor), Extinctions. Univ. Chicago Press, Chicago, Illinois.

- . 1986. Patterns of change in plant communities through geological time. Pp. 126–141 in J. Diamond & T. Case (editors), *Community Ecology*. Harper and Row, New York.
- & K. J. NIKLAS. 1987. Adaptation, plant evolution, and the fossil record. *Rev. Palaeobot. Palynol.* 50: 127–149.
- & G. W. ROTHWELL. 1981. Paleobotany: perspectives in 1980. *Paleobiology* 7: 7–35.
- , K. J. NIKLAS, P. G. GENSEL & B. H. TIFFNEY. 1984. Character diversification and patterns of evolution in early vascular plants. *Paleobiology* 10: 34–47.
- KRASSILOV, V. A. 1975. *Paleoecology of Terrestrial Plants*. John Wiley and Sons, New York.
- LLOYD, M. & R. J. GHELARDI. 1964. A table for calculating the "equitability" component of species diversity. *J. Anim. Ecol.* 33: 217–225.
- NICHOLS, J. D. & K. H. POLLOCK. 1983. Estimating taxonomic diversity, extinction rates, and speciation rates from fossil data using capture-recapture models. *Paleobiology* 9: 150–163.
- NIKLAS, K. J. 1987. Large-scale changes in animal and plant terrestrial communities. Pp. 383–404 in D. Jablonski & D. M. Raup (editors), *Patterns and Processes in the History of Life (Dahlem Konferenzen 1984)*. Springer-Verlag, Berlin.
- , B. H. TIFFNEY & A. H. KNOLL. 1980. Apparent changes in the diversity of fossil plants: a preliminary assessment. Pp. 1–84 in M. K. Hecht, W. C. Steere & B. Wallace (editors), *Evolutionary Biology, Volume 12*. Plenum Press, New York.
- , ——— & ———. 1985. Patterns in vascular land plant diversification: an analysis at the species level. Pp. 97–128 in J. W. Valentine (editor), *Phanerozoic Diversity Patterns*. Princeton Univ. Press, Princeton, New Jersey.
- PADIAN, K. & W. A. CLEMENS. 1985. Terrestrial vertebrate diversity: episodes and insights. Pp. 41–96 in J. W. Valentine (editor), *Phanerozoic Diversity Patterns*. Princeton Univ. Press, Princeton, New Jersey.
- PEASE, G. M. 1985. Biases in the durations and diversities of fossil taxa. *Paleobiology* 11: 272–292.
- PHILLIPS, T. L. 1974. Evolution and vegetative morphology in coenopterid ferns. *Ann. Missouri Bot. Garden* 61: 427–461.
- & W. A. DIMICHELE. 1981. Paleoecology of Middle Pennsylvanian age coal swamps in southern Illinois—Herrin Coal Member of Sahara Mine No. 6. Pp. 231–284 in K. J. Niklas (editor), *Paleobotany, Paleoecology, and Evolution*. Praeger Press, New York.
- PIELOU, E. C. 1977. *Mathematical Ecology*, 2nd edition. John Wiley and Sons, New York.
- RAUP, D. M. 1976. Species diversity in the Phanerozoic: an interpretation. *Paleobiology* 2: 289–297.
- . 1979. Biases in the fossil record of species and genera. *Bull. Carnegie Mus. Nat. Hist.* 13: 85–91.
- . 1983. On the early origins of major biological groups. *Paleobiology* 9: 107–115.
- & J. J. SEPKOSKI, JR. 1982. Mass extinctions in the marine fossil record. *Science* 215: 1501–1503.
- & ———. 1984. Periodicity of extinctions in the geological past. *Proc. Natl. Acad. U.S.A.* 81: 801–805.
- & ———. 1986. Periodic extinction of families and genera. *Science* 231: 833–836.
- & S. M. STANLEY. 1971. *Principles of Paleontology*. W. H. Freeman and Company, San Francisco, California.
- RAVEN, J. A. 1986. Evolution of plant life forms. Pp. 421–492 in T. J. Givnish (editor), *On the Economy of Plant Form and Function*. Cambridge Univ. Press, Cambridge.
- RUDWICK, M. J. S. 1976. *The Meaning of Fossils*. Science History Publications, New York.
- SCHOPF, T. J. M., D. M. RAUP, S. J. GOULD & D. S. SIMBERLOFF. 1975. Genomic versus morphological rates of evolution: influence of morphologic complexity. *Paleobiology* 1: 63–70.
- SEPKOSKI, J. J., JR. 1980. The three great evolutionary faunas of the Phanerozoic marine fossil record. *Geol. Soc. Amer. Abs. with Program* 12: 520.
- . 1981a. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology* 7: 36–53.
- . 1981b. The uniqueness of the Cambrian fauna. Pp. 203–207 in M. E. Taylor (editor), *Short Papers for the Second International Symposium on the Cambrian System*. U.S. Geol. Surv. Open-File Rep. 81-743.
- . 1984. A kinetic model of Phanerozoic taxonomic diversity. III. Post Paleozoic families and mass extinctions. *Paleobiology* 10: 246–267.
- , R. K. BOMBACH, D. M. RAUP & J. W. VALENTINE. 1981. Phanerozoic marine diversity and the fossil record. *Nature (London)* 293: 435–437.
- SIGNOR, P. W. & J. W. LIPPS. 1982. Sampling bias, gradual extinction patterns and catastrophes in the fossil record. *Geol. Soc. Amer., Special Pap.* 190: 291–296.
- SOBER, E. 1985. *The Nature of Selection*. MIT Press, Cambridge, Massachusetts.
- SPICER, R. A. & C. R. HILL. 1979. Principal components and correspondence analyses of quantitative data from a Jurassic plant bed. *Rev. Palaeobot. Palynol.* 28: 273–299.
- STEWART, W. N. 1983. *Paleobotany and the Evolution of Plants*. Cambridge Univ. Press, Cambridge.
- TIFFNEY, B. H. 1981. Diversity and major events in the evolution of land plants. Pp. 193–280 in K. J. Niklas (editor), *Paleobotany, Paleoecology, and Evolution, Volume II*. Praeger Publishers, New York.
- & K. J. NIKLAS. 1985. Clonal growth in land plants: a paleobotanical perspective. Pp. 35–66 in J. B. C. Jackson, L. W. Buss & R. E. Cook (editors), *Population Biology and Evolution of Clonal Organisms*. Yale Univ. Press, New Haven, Connecticut.
- WHITE, J. 1979. The plant as a metapopulation. *Ann. Rev. Ecol. Syst.* 10: 109–145.
- WHITTAKER, R. H. 1977. Evolution of species diversity in land communities. Pp. 1–68 in M. K. Hecht, W. C. Steere, B. Wallace (editors), *Evolutionary Biology, Volume 10*. Plenum Press, New York.